

THE TADPOLE OF THE COSTA RICAN
FRINGE-LIMBED TREE-FROG,
HYLA FIMBRIMEMBRA

Jay M. Savage

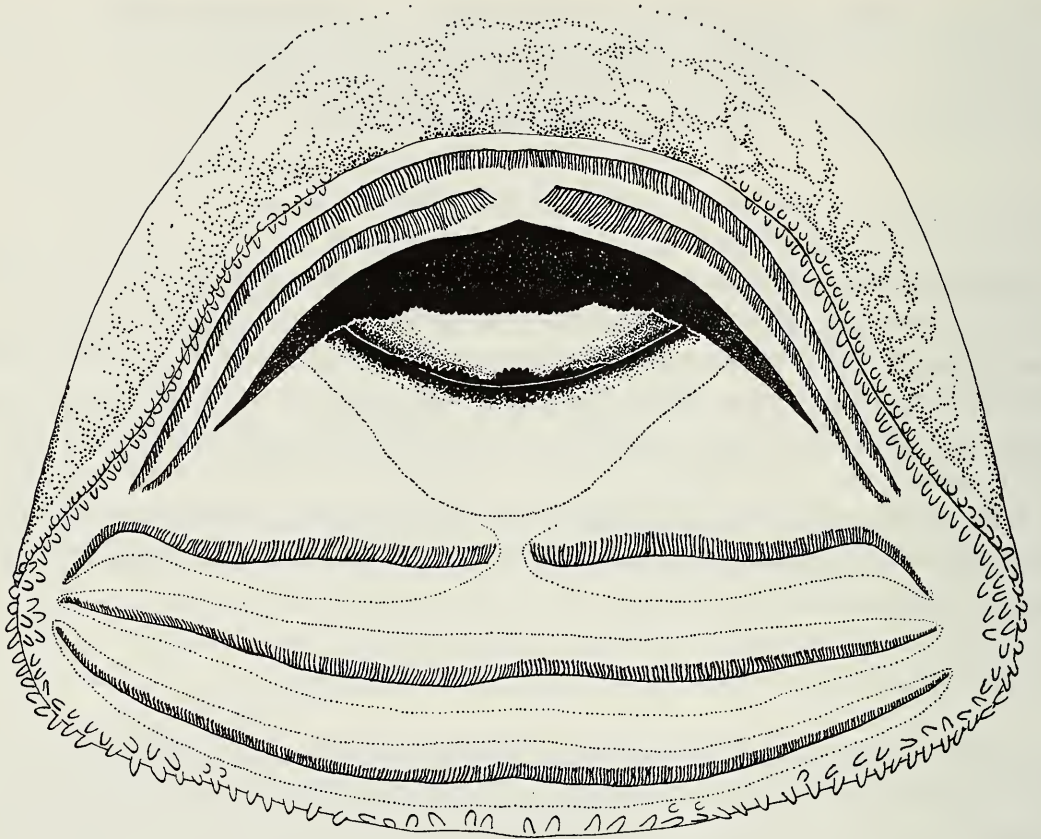
Abstract.—A single large, long-tailed, tuberculate, and generalized hylid tadpole from the Isla Bonita-Cinchona area of the Cordillera Central of Costa Rica cannot be associated with any of the 93 tadpoles of the family Hylidae described from Mexico and Central America. Consideration of geography and tadpole characteristics typical of the species groups for the 29 hylid species from the region, whose tadpoles are unknown, leads to association of the larva with the fringe-limbed flying frog, *Hyla fimbriembra*. The tadpole is the first to be described for the 5 species of flying frogs that comprise the *miliaria* group.

In 1963 Norman J. Scott and I collected a single large tadpole from the La Cinchona area of the Cordillera Central of Costa Rica made famous by Edward H. Taylor as the type locality of many amphibians and reptiles (see Savage, 1974). The tadpole was peculiar in the combination of small labial disk, very long tail (77% of total length) and peculiarly tuberculate flanks. The understanding of the characteristics of tadpoles of most Costa Rican anurans was minimal at that time and it was not possible to hazard a guess at our example's identity.

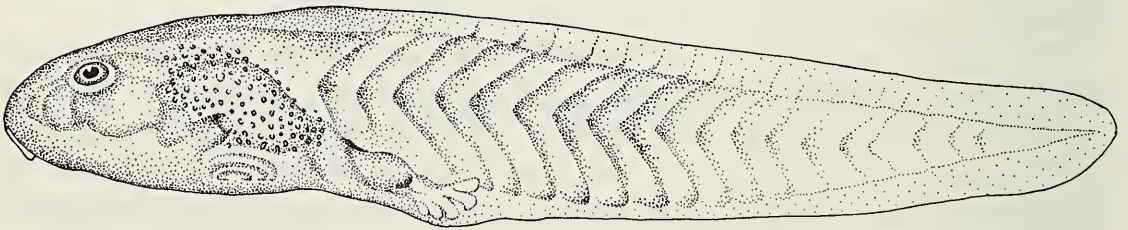
Fortunately, the intervening years have seen the knowledge of larval stages for Costa Rican anurans increase several fold and tadpoles for most species, except the many forms in the genera *Bufo* and *Centrolenella*, are now known. In the course of preparing a review of the tadpoles of Costa Rican frogs and toads, I have again turned to an attempt at associating the Cinchona example (Fig. 1) with a named adult population.

The example in question was collected at Costa Rica: Provincia de Alajuela: Canton Alajuela: Cinchona (1,360 m) by Jay M. Savage and Norman J. Scott on 26 September 1963, between 8:30 and 10:00 P.M. It is number 7015 in the CRE collection at the University of Southern California. Its salient features are summarized below, using the terminology of Duellman (1970:33-43), where applicable.

General Features.—Stage 38 (system of Gosner, 1960). Body robust, width somewhat greater than depth. Nostrils directed anteriolaterally, eyes directed laterally. Anus dextral; spiracle sinistral, located on side of body below level of eye, about ½ of distance from eye to posterior margin of



.6mm



8mm

Fig. 1. Tadpole of *Hyla fimbriembra*. Upper, oral disk; lower, lateral view.

body. Lateral area of posterior portion of body heavily tuberculate. Caudal fin extending onto body as a low ridge that reaches almost to level of spiracle; dorsal portion about $\frac{1}{3}$ depth of caudal musculature, ventral portion reduced; fin rounded at end.

Oral disk small, anteroventral, directed ventrally. Disk complete, not indented laterally; disk bordered laterally by 2–3 rows of small papillae, below by 1 row; oral papillae incomplete across upper labium. Upper beak a narrow arch, lower beak less well-developed, both with small serrations. Denticles in 2/3 rows, row immediately above upper beak interrupted medially, uppermost row and row just below lower beak longest, about equal in length, others only slightly shorter.

Coloration.—Dorsum and sides of head uniform brown, gradually grading into dirty white venter; flanks lightly pigmented but appear black because black parietal peritoneum visible through skin. Hindlimb rudiment strongly barred with black above. Tail musculature light pinkish tan; caudal fins and overlying skin transparent with distinct network of mottled black pigment.

Measurements (mm).—Standard length (body length) 17; tail length 57; total length 74; tail length 77% of total length.

An Attempt at Identification

At the present time Costa Rica has a known anuran fauna of approximately 120 species. Thirty-three of these forms, all members of the genus *Eleutherodactylus*, are either known to have direct development without a tadpole stage or are presumed to share this feature in common, as far as known with all approximately 300 members of the genus. The remaining species are allocated to 8 frog families as follows, with the denominator indicating the number of Costa Rican species in the family, and the numerator the number for which tadpoles have been described: Rhinophrynidae (1/1); Microhylidae (1/3); Leptodactylidae (6/6); Bufonidae (5/14); Hylidae (34/39); Dendrobatidae (5/7); Centrolenidae (7/13); and Ranidae (4/4).

The characteristics of the Cinchona example do not match the description of any known tadpole from Costa Rica or from adjacent areas of Central America. It must therefore represent a known species for which the tadpole is not known or an unknown species. If one follows a process of elimination based on the available data, the number of feasible alternative possibilities can be substantially reduced. In the following comparisons, features for the unnamed tadpole are indicated in parentheses.

There is little likelihood that the mystery tadpole represents an undescribed species of either the Rhinophrynidae or Microhylidae. All known members of these families have tadpoles that lack beaks and denticles and have either two spiracles or a single ventrally located one (beaks and denticles present; a single sinistral spiracle).

Members of the family Ranidae are also excluded from consideration since the tadpoles of all known Central American species have been described and have either the oral disk indented laterally (*Pipiens* group) or high numbers of denticle rows $3/4$ to $6/4$ (complete oral disk and denticle rows $2/3$).

The tadpoles of members of the genera *Atelopus* and *Bufo* (family Bufonidae) are distinctive and cannot be confused with the present specimen. *Atelopus* has a well-developed ventral disk (no ventral disk) and *Bufo* has the oral papillae incomplete on upper and lower labia (complete on lower labium).

The Centrolenidae may also be eliminated from consideration since all known tadpoles of this family have a median anus, very short denticle row segments just above the mouth that are separated from one another by a huge gap above the beak and are pale pink to bright red (in life) with minimal dark pigment (dextral anus, only a narrow gap in long denticle row segments just above beak, and with considerable dark pigmentation).

Members of the family Leptodactylidae known from lower Central America that have free-living larvae may also be eliminated from consideration. *Leptodactylus* has a median anus (dextral); *Physalaemus* has the oral disk indented laterally (oral disk complete) and *Pleurodema* has a median anus (dextral).

Members of the family Dendrobatidae show a considerable diversity of larval features (Savage, 1968; Silverstone, 1975, 1976). In known *Phyllobates* and most *Colostethus* the oral disk is indented laterally (oral disk complete). In most *Dendrobates* the anus is median (dextral) but in those with a dextral anus the oral disk is indented (oral disk complete). In the Costa Rican form *Colostethus nubicola* which has a non-indented umbelliform oral disk (complete but non-umbelliform oral disk) the anus is dextral and denticle rows are absent ($2/3$ denticle rows). The tadpole of *Dendrobates pumilio* of Costa Rica also has a complete oral disk but has a median anus (dextral) and 0- $1/2$ -2 rows of denticles ($2/3$ rows of denticles).

The mystery tadpole has been compared directly to tadpoles of all lower Central American species for which tadpoles are known in the 7 families discussed above. There can be little doubt that it is distinct from all of them and almost certainly does not represent an undescribed species or any known species for which the tadpole remains unknown at this time. This comparison eliminates from serious consideration as the possible congeners of the tadpole representatives of all the lower Central American genera of these families except for the monotypic bufonid *Crepidophryne*. No tadpole is known for this genus which seems to be a specialized derivative from *Bufo* (Savage and Kluge, 1961). Most likely, if the species has a tadpole stage, it would agree with *Bufo*, which uniformly has the oral disk indented laterally and the oral papillae broadly interrupted across both the upper and

lower labia (oral disk complete; complete series of papillae across lower labia). In addition, *Crepidophryne* is known from only a few localities in the Cordillera de Talamanca (Savage, 1972), the closest some 75 km southeast of the collecting site for the unknown larvae.

The unidentified tadpole agrees in basic features with generalized tadpoles of species in the large family Hylidae, the only family not eliminated from consideration in the above review. These basic features include: complete oral disk, dextral anus, sinistral spiracle located laterally, denticles 2/3, and oral papillae incomplete across upper and complete across lower labium. Among the hylids of lower Central America, 5 members of the genus *Hyla* (*angustilineata*, *elaeochroa*, *loquax*, *pseudopuma* and *staufferi*) and 4 members of the genus *Smilisca* (*baudinii*, *phaeota*, *puma* and *sila*) resemble the Cinchona tadpole in these basic features. Direct comparison of comparable stages of tadpoles of these 9 forms to the unnamed larva clearly indicates that it cannot be associated with any of them. It may most easily be separated from *H. elaeochroa* and *H. staufferi* by the shape of the body and fin form. In the latter 2 species the body is deep, with the depth much greater than width and the tail fins are deep, with upper and lower portions much deeper than tail musculature, and taper to a point (body ovoid, depth and width about equal; depth of upper and lower portions of caudal fin less than depth of tail musculature and tip of fin rounded). *H. loquax*, *S. baudinii* and *S. phaeota* most obviously differ from the Cinchona tadpole in having smooth bodies (tuberculate). *H. angustilineata*, *H. pseudopuma* and *S. sila* do not have the dorsal portion of the fin extending onto the body (fin extending onto body).

The above review indicates that the mystery tadpole represents a species of the tree-frog family Hylidae. An analysis of the characteristics of the larvae of this family from Mexico and Central America, almost all of which are so ably described and illustrated by Duellman (1970), confirms this view. Of 122 hylid species now recognized from the region, the tadpoles of 29 remain undescribed. Most of the species (20) for which tadpole data are lacking occur in the highlands of southern Mexico and Guatemala (15) or are inhabitants (5) of sites in western Mexico (one of these forms reaches Guatemala and El Salvador). All of these species are found at sites far removed geographically and ecologically from the Cordillera Central of Costa Rica.

Of the remaining 9 forms without known tadpoles, all from lower Central America, three species, *Agalychnis calcarifer* and *A. litodryas* and *Phyllomedusa venusta*, belong to genera whose tadpoles are so distinctive as to eliminate them from consideration. Tadpoles for these genera uniformly have the spiracle located ventrally although sinistral to the midventral region and have a pointed tail fin (lateral spiracle and rounded tail fin). One form, *Hyla pugnax* of the Pacific lowlands in western Panama and northern Co-

lombia (Kluge, 1979) belongs to a species group in which all known tadpoles have 2/4 denticle rows.

The elimination of the 4 mentioned species from consideration leaves 4 forms, *Hyla fimbriembra*, *H. lythrodes*, *H. miliaria* and *H. xanthosticta*, all known from Costa Rica, and *H. thysanota*, known only from extreme eastern Panama, as candidates for association with the tadpole. *H. lythrodes* and *xanthosticta*, each known from a single male holotype, are unlikely to be conspecific with the tadpole. All of the allies of these two forms (Savage, 1967; Duellman, 1970) have larvae with oral papillae complete across the upper labium (incomplete). Direct comparison of the Cinchona tadpole with known tadpoles of these 7 allied forms convinces me that they are not related. Additional differences include: *H. rufioculis* and *uranochroa*, 2/2 denticle rows (2/3); *H. legleri*, 2/5 denticle rows (2/3); *H. rivularis*, *pictipes* and *tica*, 4–7 rows of papillae on lower labium (1); and *H. debilis*, body depressed (ovoid). *H. lythrodes* is most similar to *rufioculis* and *xanthosticta* to *pictipes* in adult features.

The analysis leaves only the Costa Rica and Panama members of the *Hyla miliaria* group (Duellman, 1970) (*fimbriembra*, *miliaria*, and *Thysanota*) as probable adult representatives of the mystery tadpole. Significantly, the tadpole of no member of this distinctive group of large frogs has ever been described. The group as currently understood contains 5 species: *echinata* of southern Mexico; *fimbriembra* of Costa Rica; *miliaria* of Nicaragua, Costa Rica, Panama and Colombia; *thysanota* of eastern Panama; and *valancifer* of southeastern Mexico and Guatemala. Only the 2 Costa Rican species seem reasonable candidates for association with the Cinchona tadpole.

Of the 2 forms, it is clear that the tadpole almost certainly is *H. fimbriembra*. This species is known from only 2 specimens (Duellman, 1970) an adult female (the holotype) and a juvenile male (the holotype of the name *H. richardtaylori*). Both examples were collected in the Isla Bonita–Cinchona area (Savage, 1974), a few kilometers apart, by Edward H. Taylor (1948). The tadpole subject of this paper was collected virtually at the type locality of *fimbriembra*. *Hyla miliaria*, on the other hand, is known only from one locality, at 600 m elevation in Costa Rica.

Adult members of the *miliaria* group are very large (known to reach 106 mm in male *miliaria*) frogs with immense hands and feet that are extensively webbed. In addition the outer margins of the hands, forearms, and feet have extensive fleshy fringes. Known adult males have the prepollex modified as a projecting spine (*miliaria*), a spadelike plate (*valancifer*), or clump of spines (*echinata*). Duellman (1970) has described and illustrated the use of the hands, feet, webs and fringes in the flight, or more accurately glide, in an example of *miliaria*. All known juveniles of the group have a tuberculate dorsum and the unique and extensively tuberculate body of the tadpole here

associated with *H. fimbrimembra* is another confirmation of the correctness of this allocation. I have seen no other hylid tadpole from Mesoamerica having this condition.

Certainly adults of the *miliaria* stock are among the rarest and most bizarre of New World tree-frogs. The tadpole of *H. fimbrimembra* is quite ordinary and shares basic character combinations with many other hylids. This situation offers support for Starrett's Rule which states that the most specialized and uniquely modified tadpoles develop into ordinary frogs whereas the most bizarre and distinctive frogs have ordinary, generalized tadpoles.

Acknowledgments

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Finally, I wish especially to acknowledge the advice on, and insight into, tadpole biology provided over the past 20 some years by my colleague, the discoverer of Starrett's Rule, Dr. P. H. "Holly" Starrett.

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